

Recovery responses of two benthic assemblages following an acute hypoxic event on the Texas continental shelf, northwestern Gulf of Mexico

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Abstract: A hypoxic/anoxic event occurred in the northwestern Gulf of Mexico between May and July 1979. This event, associated with warm water temperatures, water column stratification and the decay of a phytoplankton bloom, led to the production of hydrogen sulphide which moved above the sediment–water interface and into the lower 2 metres of the water column. Regular monthly sampling at two sites (15 and 21 m depths) off Freeport, Texas, showed that abundances of benthic organisms declined precipitously during the event. Divers inspecting the study areas during the event observed ‘cottony’ mats, presumed to be sulphur bacteria colonies, covering large areas of bottom, and numerous bodies of dead benthic invertebrates.

Recovery of the two communities was markedly different. The assemblage in deeper water apparently stabilized within a year; the species of polychaetous annelids that were dominant before the event quickly returned to dominance and there was very little evidence of succession of different species during the recovery process. The shallower water assemblage, however, underwent a very different recovery process. Following the hypoxic event, polychaete dominance was greatly reduced, and there occurred successional dominance which involved several species in different taxa. Each of these species underwent a ‘bloom’ and constituted the numerical dominant for 1 to 3 months, and then declined and was replaced by another species’ ‘bloom’. This sequential dominance pattern persisted until about May 1981, two years after the hypoxic event, at which time polychaetes again became, and remained, numerically dominant.

Hypoxia (<2.0 ppm O₂) and anoxia (0.0 ppm O₂) are common occurrences in some localities and episodic events in others. In the Gulf of Mexico west of the Mississippi Delta, the continental shelf of Louisiana apparently experiences hypoxia almost annually, although the extent of the affected area varies from year to year (Gaston 1985; Gaston, *et al.* 1985; Renaud 1986; Pokryfki & Randall 1987; Boesch *et al.* this volume; Rabalais *et al.* this volume). The Texas coast, however, apparently is affected infrequently (Harper *et al.* 1981; Rabalais *et al.* this volume).

If anoxia is prolonged, conditions at the sediment–water interface, and in the water column above, may permit survival of sulphate reducing bacteria, normally found deeper in sediments (Jørgensen 1980); these bacteria produce hydrogen sulphide, which is toxic to

aerobic life, as a metabolic by-product. Unfortunately such events are fairly unpredictable as to timing and location, and the phenomenon may have nearly run its course before it is detected and can be studied. Hypoxic events that occur in the midst of an ongoing study, allowing investigators to determine effects on communities and to follow the process of recovery, are rare. We were extremely fortunate to have been studying two benthic assemblages off the upper Texas coast when an hypoxic event occurred in 1979. This study, which began in September 1977 and terminated in May 1984, gave us two years of pre-hypoxia data and five years of post-hypoxia data, allowing us to monitor the recovery process.

The hypoxic event, and its immediate consequences, were documented in a previous paper (Harper *et al.* 1981). We postulated that a combination of decay of a phytoplankton bloom and water column stratification induced by warm water and a strong salinity gradient (especially in June 1979 as shown by cross-shelf salinity data (Kelly & Randall 1980)), caused hypoxia to occur in bottom waters over a large part of the inner shelf of the upper Texas coast. The

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bloom may have originated in Louisiana waters and moved westward with the prevailing currents, as did a subsequent bloom with which benthic mortalities were associated (Harper & Guillen 1989). Bacterial decomposition of dead phytoplankton cells reduced oxygen levels in bottom waters sufficiently to allow anaerobic, sulphur-reducing bacteria, to survive in the upper sediment layers. These bacteria generated hydrogen sulphide (which research divers, while working on the bottom, could 'smell' in the water seeping into their masks) and may have been responsible for much of the benthic mortalities. Large patches of cottony-appearing material, thought to be sulphur bacteria colonies, were seen on the bottom and dead benthic organisms littered the bottom at most stations (cf. photographs in Stachowitsch 1983). Organisms on East Bank, a rock reef in the study area, were found to be dead or dying. Nektonic abundances were very low in the hypoxic area, indicating that motile organisms migrated away from the affected region (Pavella *et al.* 1983).

Hypoxic conditions were broken up at the shallower nearshore site by Tropical Storm Claudette in August 1979, and the deeper site became normoxic shortly after. Following re-establishment of normoxic conditions, there was an irruption of benthic organisms, predominantly the polychaete *Paraprionospio pinnata* (Spionidae), which lasted approximately one month and was then followed by a rapid decline. This report describes the changes in community structure at the two study sites during the recovery phase.

Study areas

As noted above, two sites were investigated, both offshore from Freeport, Texas, on the upper Texas coast (Fig. 1). The study was part of a multidisciplinary project designed to determine if the discharge of large volumes of brine from salt dome excavation produced a measurable impact on the offshore environment. The shallower nearshore site, about 8 km off Freeport in 15 m depth, was on the subaqueous delta of the Brazos River and sediments were reddish to brownish silts and clays. The offshore site, about 19 km off Freeport in 21 m depth, was located on a drowned Pleistocene delta of the Brazos–Colorado River and sediments were sandy mud to muddy sand. The nearshore site was the locality first selected for the brine discharge system. It was, however, in the white shrimp (*Penaeus setiferus*) spawning grounds, and vociferous opposition by shrimp fishermen and environmentally concerned indi-

viduals caused the discharge system to be moved to the offshore site. We succeeded in retaining the nearshore site as a 'control' sampling area.

Methods

Samples were collected by divers using three Ekman grabs (232 cm² each) attached to a line. The line had an anchor at one end and a buoy at the other. When the research vessel came on station, the sampler array was dropped overboard, the divers entered the water holding the line and were pulled to the bottom by the anchor. On bottom, each sampler was moved to an undisturbed location, pushed into the bottom, triggered, and the vent flaps secured by an elastic band. The divers also collected a water sample from just above the sediment–water interface using a van Dorn sampler attached to their scuba cylinder, and a sediment sample in a plastic jar. If conditions permitted, the divers made a visual assessment of bottom conditions. The sampling array was returned to the surface by a lift bag, and was then pulled aboard the vessel by the deck crew. Each sample was washed separately on a 0.5 mm mesh sieve and the retained material was placed in a jar and fixed with 5% seawater–formalin. Temperature and salinity of surface and bottom water samples were determined using YSI Model 33 T-S-C meter, and dissolved oxygen (D.O.) was measured using a YSI Model 57 dissolved oxygen meter. Temperatures of diver-collected sediment samples were measured using a Celsius thermometer.

In the laboratory, each benthic sample was washed on a 0.5 mm mesh sieve, then preserved in 70% rose bengal-stained ethanol. After at least 24 hours in the stain, each sample was washed and examined using dissecting microscopes. Organisms were removed, identified and counted. After the diffuser system began operating, sediment samples were allowed to stand 24 hours and then pore water salinities were determined using an American Optical Refractometer.

Initially, each sampling site consist of 15 stations in relatively close proximity (Fig. 1). Additional stations were added to the offshore site at two different times, but data from these additional stations have not been incorporated in this report. Budgetary constraints forced reduction in sampling effort at the nearshore site in March 1982. Five stations, A3, A5, A6, D2 and E2, continued to be sampled and abundance data from these collections have been extrapolated to 15-station data sets.

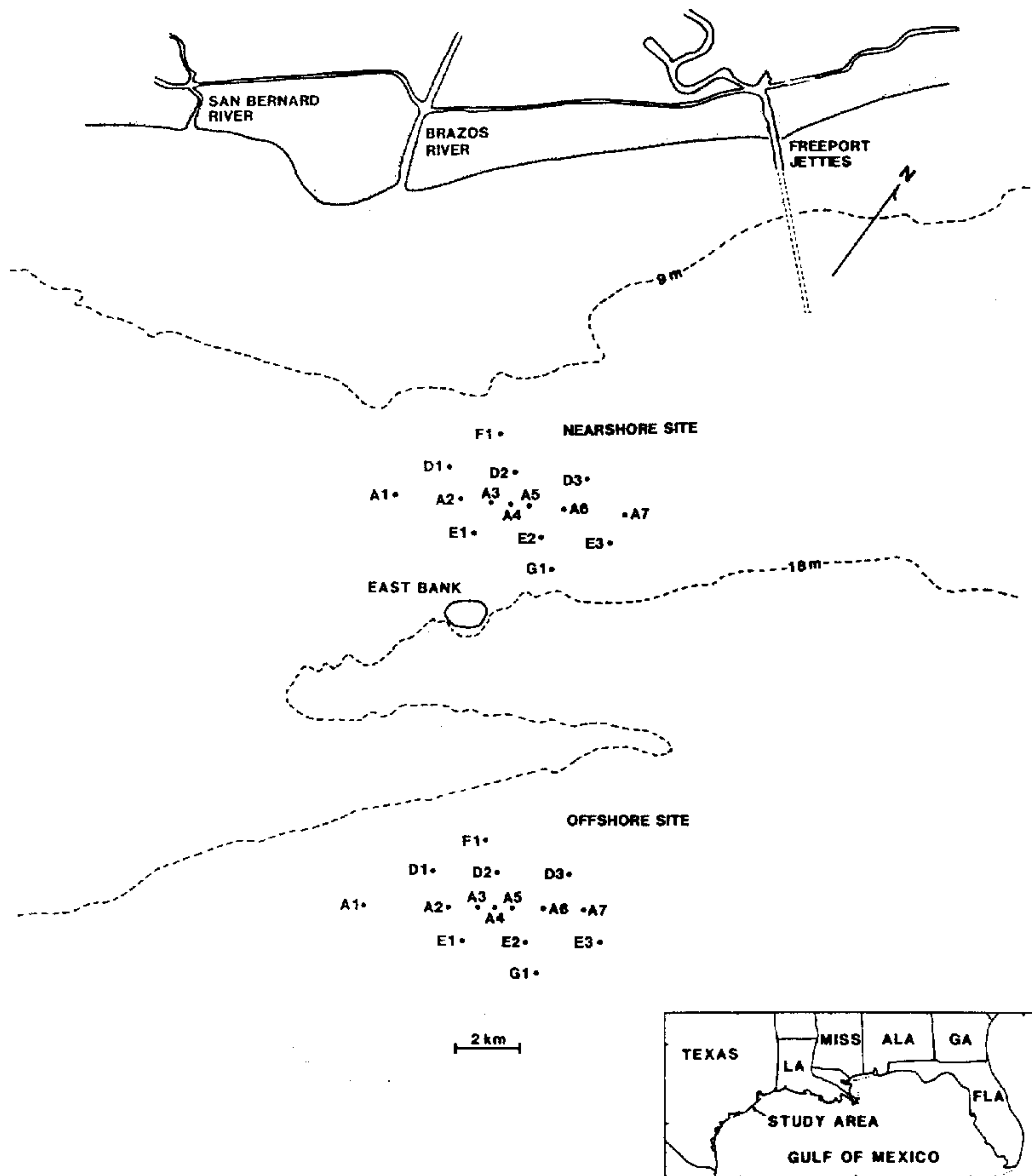


Fig. 1. Map of the area off Freeport, Texas, showing locations of sampling stations at the nearshore and offshore study areas.

Results: abiotic characteristics

Temperature

Temperature trends were similar at both study areas and among years. Sediment temperatures usually ranged from about 15°C in the winter to 30°C in the summer at the offshore site and 12 to 30°C at the nearshore site (Fig. 2), and these

temperatures tended to lag behind the bottom water temperature (Appendix 1). There also were lag phases in the spring and fall in which the bottom water temperature increased and decreased more slowly than the surface water temperatures; this lag was most noticeable at the deeper offshore site (Appendix 1). Offshore bottom water temperature trends show a slight decrease in June or July of each year, suggesting

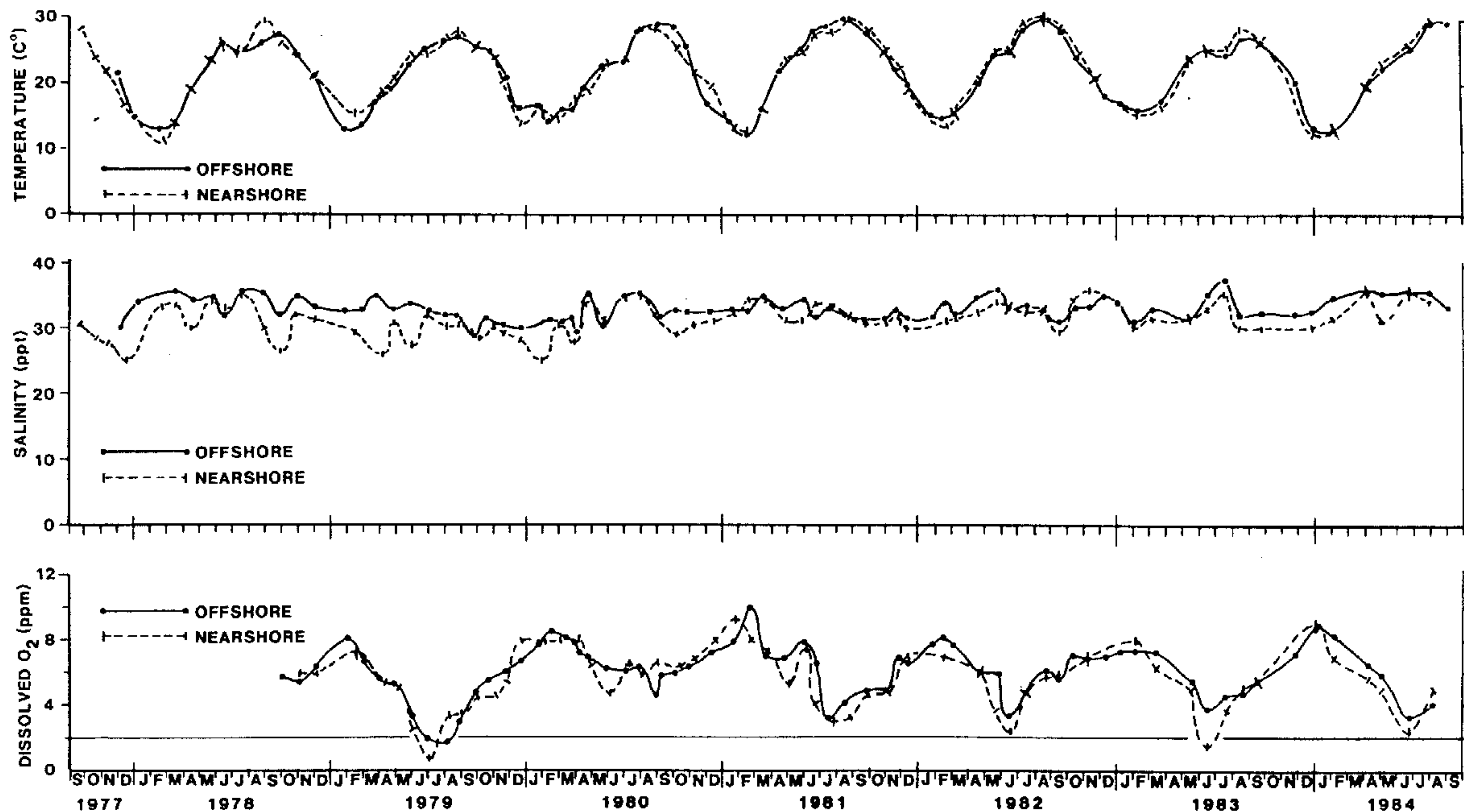


Fig. 2. Temporal trends of mean values of sediment temperatures, bottom water salinities and bottom water dissolved oxygen concentrations at the nearshore and offshore study areas.

influx of deeper, colder water associated with an upwelling event (such an event is evident in shelf-wide data collected by the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) in 1963–65 (Temple *et al.* 1977)).

Salinity

Bottom water salinities at the offshore site were fairly uniform during the entire study period and were usually above 30‰ (Fig. 2). After the diffuser system began discharging high volumes of brine there were instances when the bottom water salinity was elevated above oceanic salinities. Strong salinity gradients occurred in April–July of 1979, and were associated with the occurrence of hypoxia in June and July (Appendix 1).

Bottom water salinities at the nearshore site were much more variable than at the offshore site (Fig. 2), and there was a greater probability of decreased salinity when surface salinities decreased (Appendix 1). There were five instances of strong stratification during the study, i.e. June 1979, May 1980, June 1981, May 1982 and June 1983 (Appendix 1). Two of these (June 1979 and June 1983) coincided with, or preceded, hypoxic conditions.

Dissolved oxygen

Dissolved oxygen trends of the bottom water were similar at both sites. High concentrations (9–10 ppm) were generally recorded in the winter and lower concentrations (3–4 ppm) in summer (Fig. 2). We recorded hypoxia at both sites in June and July, 1979 (1.9 and 1.6 ppm O₂ offshore; 0.7 ppm O₂ nearshore), and at the nearshore site in June 1983 (1.5 ppm O₂). Hypoxia was also recorded at the offshore site in 1983 by Kelly *et al.* (1984); this was apparently a short-lived event that occurred between our cruises in July and August. During both recorded hypoxic events, the surface water remained oxygenated (Appendix 1). In June of 1982 and 1984, the nearshore bottom water D.O. concentration was very close to hypoxic.

Results: responses of the biota

General trends

The temporal trends of both numbers of species and of individuals were similar at both sites through most of the study period, allowing for variations because of differences in depth and substrate type (Fig. 3). At the onset of hypoxia

in May 1979, diversity and total abundance decreased. Immediately after hypoxia was broken up in August by Tropical Storm Claudette, there was a short-lived, rapid increase in species and individuals, followed by another precipitous decline. During spring 1980, diversities and total abundances reached very high levels: at the nearshore site the great abundance was chiefly due to an enormous settlement of *Abra aequalis* (Bivalvia) at three of the 15 stations. Toward the end of 1980 and through most of 1981 the diversity was about normal, but abundances were continuously very low; expected seasonal trends occurred, but the peaks were much lower than usual. Following a spring peak in 1982, the abundances at both sites returned to more normal levels. During much of the study, the population of one polychaete species, *Paraprionospio pinnata*, was so large it controlled the temporal abundance trends at both study areas (Fig. 4).

As densities of benthic organisms decreased in the latter part of 1980, the sediments at the offshore study area changed from an oxidized state to a reduced state (Slowey & Jeffrey 1984) (Fig. 5). The sediment redox potential (Eh) remained negative through 1983 with the exception of a positive spike in May 1983.

Offshore study area

The offshore assemblage was dominated by polychaete species, particularly *Paraprionospio pinnata*, for the initial 1.5 years of the study (Fig. 4), but during the four months immediately preceding hypoxia, *Ampelisca abdita* (Amphipoda) became numerically dominant and the *P. pinnata* population decreased (Fig. 6). The amphipods, however, were virtually eliminated from the assemblage by hypoxia. During the five-year period following hypoxia, polychaetes constituted >75% of the total numbers of individuals, and dominance, with a few exceptions, alternated between *P. pinnata* and *Neanthes micromma* (Polychaeta). Only one other polychaete species, *Aricidea* sp., and three non-polychaetes, *Varicorbula operculata* (Bivalvia), *Ampelisca agassizi* (Amphipoda) and *Abra aequalis* (Bivalvia) became the numerical dominant during the study period. During the 5-year post-hypoxia period, the population of *P. pinnata*, with few exceptions, constituted at least 20% of the total individuals collected.

Nearshore study area

The nearshore site assemblage, in contrast, reacted quite differently. *P. pinnata* was the con-

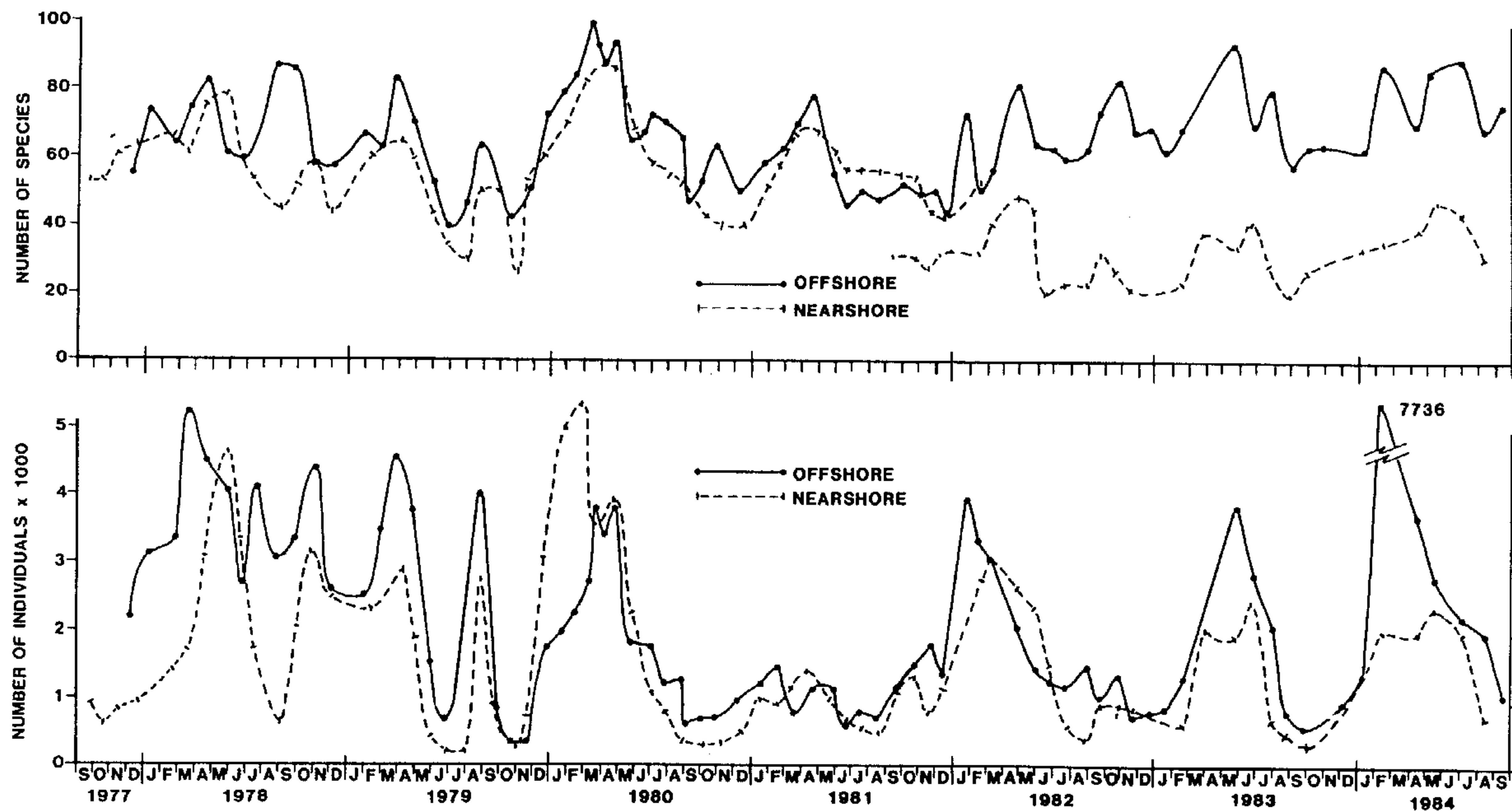


Fig. 3. Temporal trends of numbers of species and numbers of individuals in the nearshore and offshore study area benthic assemblages. Nearshore sampling reduced to 5 stations after February 1982. Species trend line based on 5 stations carried back to September 1981 for comparison with 15 station data. Abundance data after February 1982 extrapolated to 15 station data.

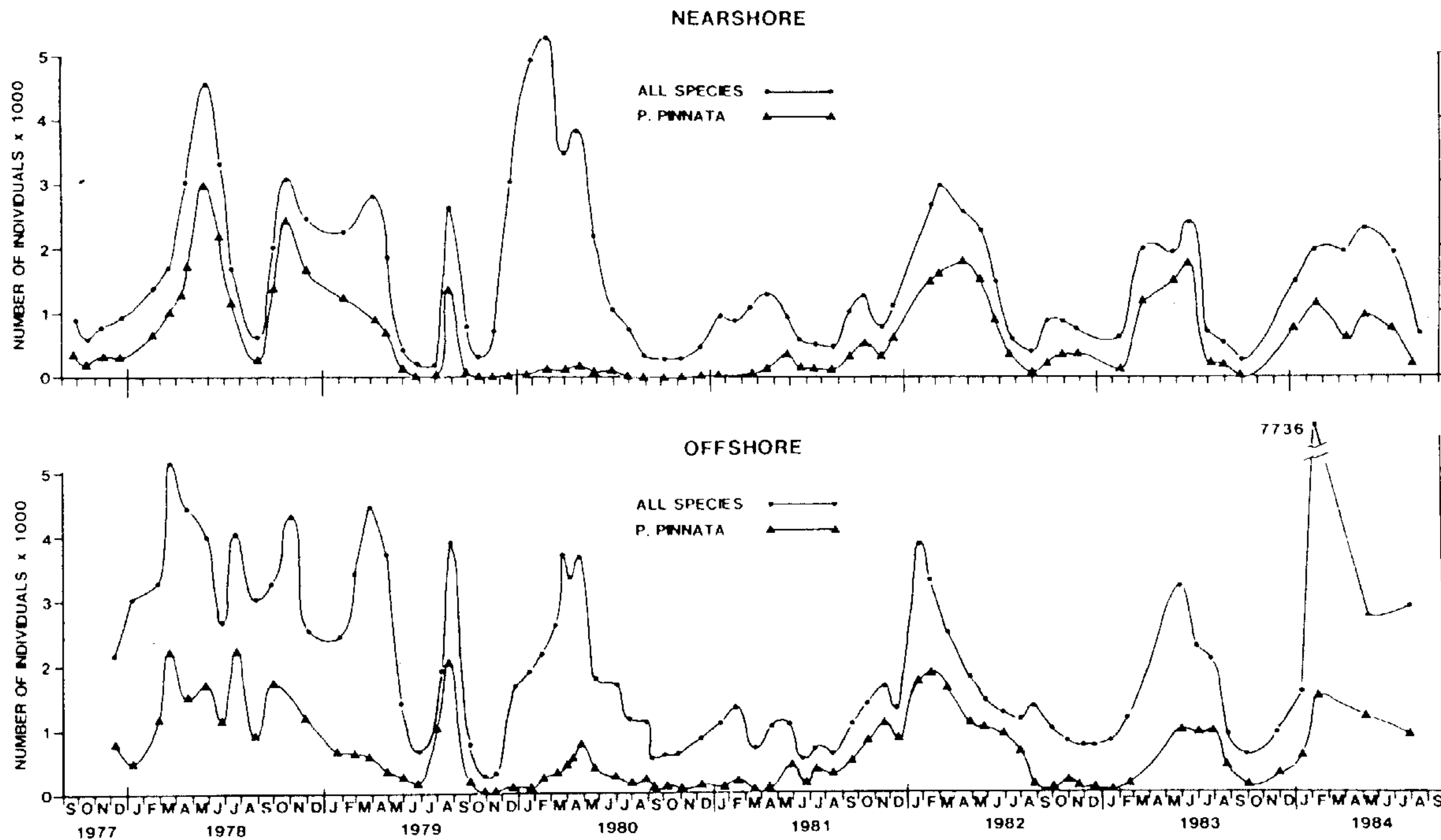


Fig. 4. Comparison of temporal abundance trends of all individuals vs. the population of *Paraprionospio pinnata* at the nearshore and offshore study areas.

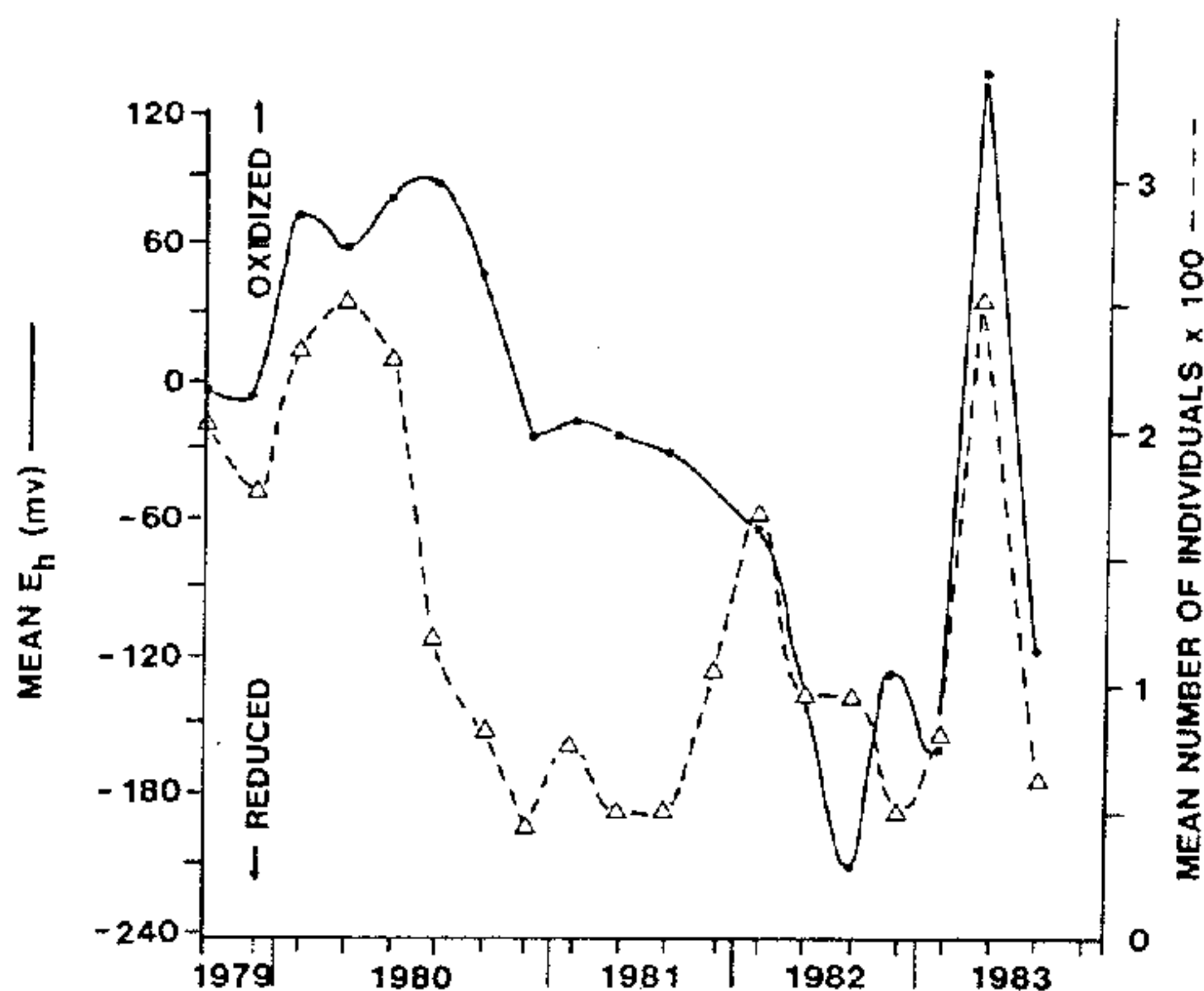


Fig. 5. Comparison of sediment Eh values (from Slowey & Jeffrey 1983) and abundances of benthic organisms at the offshore site, August 1979–August 1983.

tinuous numerical dominant from the beginning of the study until March 1979 (Fig. 4). As at the offshore site, an ampeliscid amphipod (*Ampelisca agassizi*) became dominant immediately preceding hypoxia, but virtually disappeared from the assemblage after hypoxia and was not a dominant again (Fig. 7). *P. pinnata* was the dominant for two months during and following hypoxia, including the population irruption described above. However, between October 1979 and March 1981, the population of *P. pinnata* became relatively insignificant, generally comprising less than 10% of the total abundance (but never absent) in any given month (Fig. 4). During this period, there was no prolonged dominance by any one species, but rather a succession of dominance occurred; a species 'bloomed' and became dominant for 1 to 3 months and then was replaced by another species' 'bloom.' The successional dominance involved several taxa, including Polychaeta (*Magelona* cf. *phyllisae*, (= *Magelona* sp. H) *Diopatra cuprea*), Bivalvia (*Abra aequalis*), Hemichordata (*Balanoglossus* sp.), Gastropoda (*Natica pusilla*) and Amphipoda (*Lembos brunneomaculata*), and is evident in the changes in per cent abundance of major taxa during the two year period just prior to and following hypoxia (Fig. 8).

In March 1981, *P. pinnata* again became the numerical dominant, and with three exceptions, remained so during the remainder of the study (Figs 4 & 7). The succession of dominance observed in 1980 did not recur.

Discussion

Hypoxia in bottom or near-bottom waters was recorded twice during this study, May–July 1979 and June 1983. The nearshore site bottom water may have become briefly hypoxic in June 1982 and 1984. However, only the 1979 episode coincided with great reductions in numbers of benthic organisms. This episode was the only time hydrogen sulphide was detected in the water, and only this episode was followed by the sequential dominance pattern observed at the nearshore site. The fact that bottom waters were near or below hypoxic levels during 4 of the 6 years in which D.O. was measured suggests that hypoxia may be more common in shallower, nearshore waters along the upper Texas coast than previously suspected. The data also suggest that hypoxia, *per se*, did not especially disrupt the benthic assemblages, and that anoxia/hydrogen build-up was the agent of lethality and destabilization.

Prior to hypoxia in 1979, a shift in dominance occurred at both sites. *P. pinnata* populations declined as ampeliscid amphipod populations increased. The amphipods were, however, virtually eliminated by hypoxia and, lacking planktonic larvae, did not rapidly return to the assemblages. Ampeliscids (*A. agassizi*) became dominant again in May 1983 at the offshore site, but virtually disappeared in August. As noted above, the offshore site experienced hypoxia in August, an event we did not detect because of the timing of our sampling schedule.

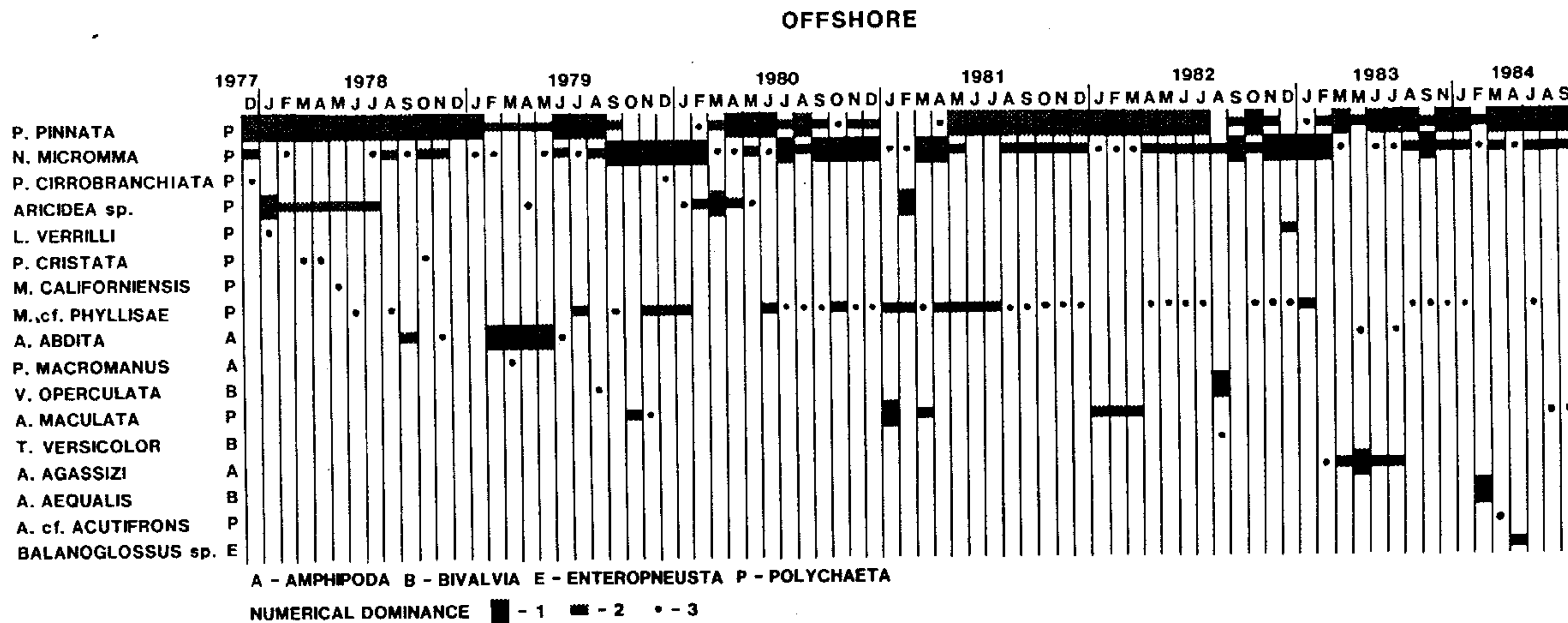


Fig. 6. First, second and third ranked numerical dominants in the offshore benthic assemblage during each sampling.

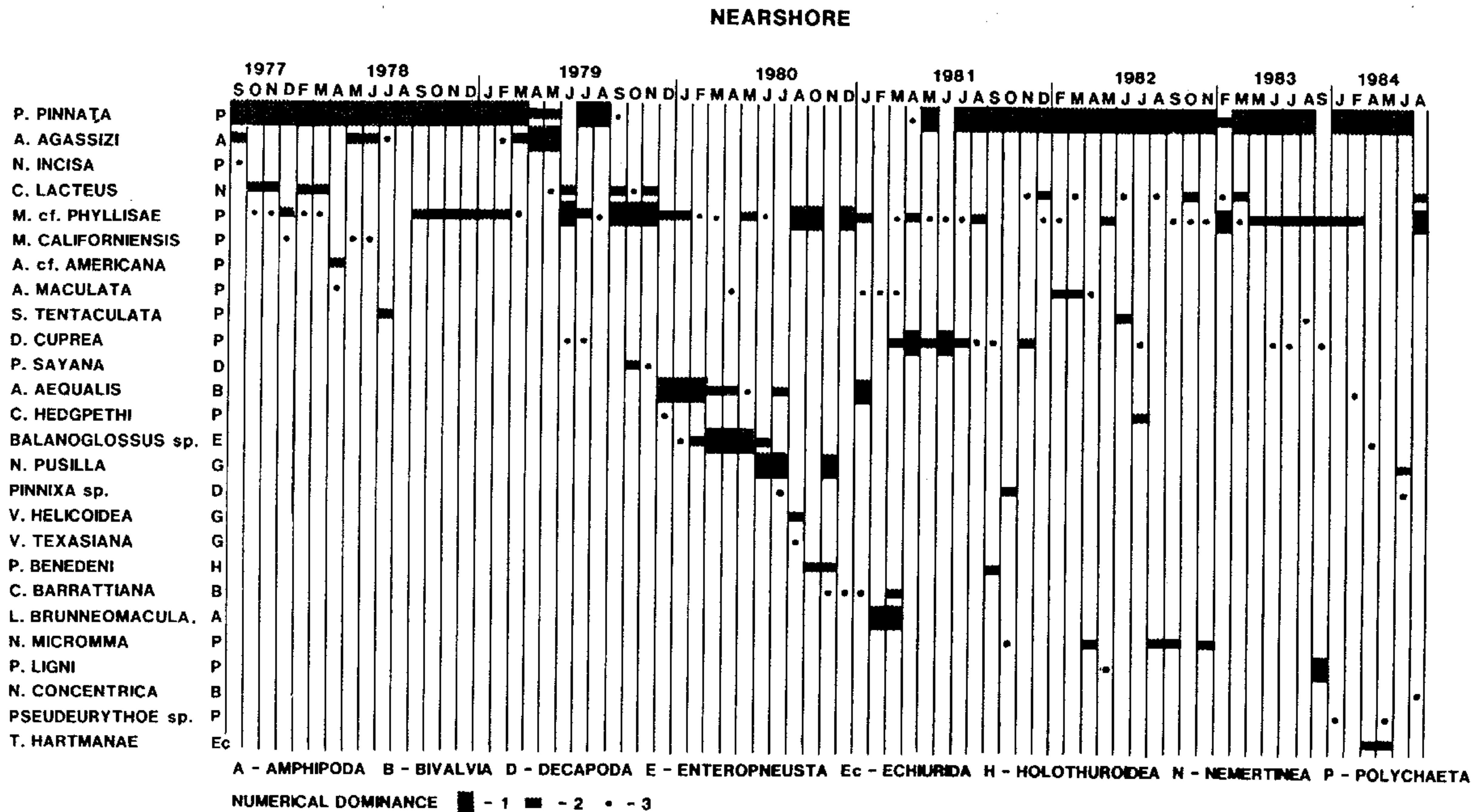


Fig. 7. First, second and third ranked numerical dominants in the nearshore benthic assemblage during each sampling.

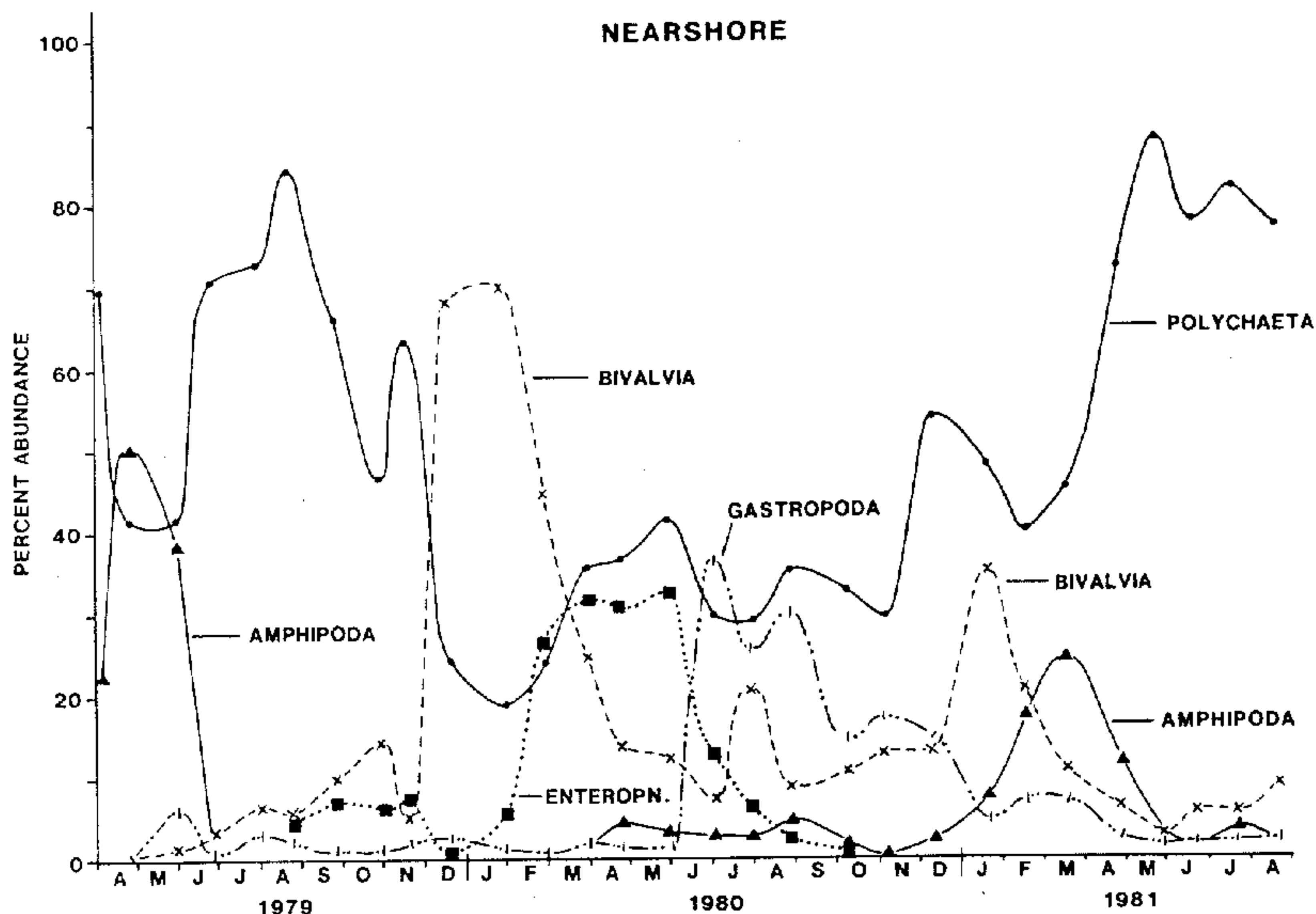


Fig. 8. Temporal trends of per cent composition of major taxa at the nearshore study area before, during and following the hypoxic event in May–July 1979.

The fact that ampeliscids became dominant only in the 2–3 months preceding both recorded occurrences of hypoxia suggests that something, perhaps an increased food supply (phytoplankton bloom?), stimulates reproduction and results in large populations occurring prior to the destruction associated with hypoxia. If this is so, ampeliscids may be useful as harbingers of incipient hypoxia, at least in the northwestern Gulf of Mexico.

The differences between the post-hypoxic responses of the two benthic assemblages are striking but the causes are not clear. Initial repopulation of nearly defaunated bottoms occurred quickly with the opportunistic species *Paraprionospio pinnata* dominating the assemblage. Most individuals in the post-hypoxic irruption were small, immature forms. Adult immigration did not appear to be important in reestablishment of the assemblage (cf. Dauer 1984). Gaston *et al.* (1985) found that experimentally defaunated sediments gained macrofaunal densities (not the same species) that equalled or exceeded the natural community in 4 to 6 weeks; these populations were dominated by opportunistic species and repopulation was mostly by larval setting. Rapid recolonization

may occur either by reproduction of survivors, or by current-transported larvae from unaffected areas. The dominant feature of the prevailing shelf circulation in the western Gulf of Mexico is an elongated cyclonic gyre (Cochrane & Kelly 1986). During most of the year, currents are downcoast (SSW) along the upper Texas coast, switching briefly to onshore in July–August with changes in prevailing winds. Unaffected populations of *P. pinnata* (which apparently produces several cohorts per year (Mayfield 1988), could have supplied larvae to repopulate the bottoms once the water was normoxic if the local population was eliminated.

The most outstanding feature of post-hypoxia is the sequential dominance that occurred at the nearshore site. This period of succession (Sept 1979–April 1980) is characterized by several features, namely: (1) the population of *P. pinnata* was very low; (2) the overall abundance of polychaetes was very low; (3) total abundances of all benthic organisms was continuously much lower than normal from August 1980 to August 1981; (4) many of the numerical dominants were molluscs (hard shells), burrowing or tubicolous; (5) the shrimp catch was one of the largest ever recorded in the statistical

areas in which the study areas fall (National Marine Fisheries Service data). We suggest that part of the cause of succession was reduction of the soft bodied polychaete populations by shrimp predation which made the bottom more available for colonization by species which were less vulnerable to predation. Reduction in abundance of shallow burrowing bioturbators is also indicated by the change in Eh from an oxidized state to a reduced state during the period of low overall abundance.

This is, however, only a partial explanation. Infaunal densities at the offshore site were also low, suggesting predation by shrimp was also occurring. The major difference is that, after the amphipod population was killed by hypoxia, polychaetes returned to their pre-hypoxic dominant status. Part of the differences may lie in the severity of impact due to hypoxia. We suspect that hypoxia first occurred in nearshore waters and spread seaward, so the nearshore site may have been exposed to hydrogen sulphide longer. Also, the recorded mean D.O. was lower nearshore (0.7 ppm) than offshore (1.6 ppm) in 1979. Another factor may be that

the nearshore site has a greater probability of recruiting larvae being carried downcoast on the 'coastal jet', and reduction of populations of surface deposit feeding spionid polychaetes (Fauchald & Jumars 1979) permitted settlement and survival of larvae which might have been eaten by the polychaetes.

Finally, the differences may be partly due to the fact that the offshore area, being deeper, is a somewhat more stable environment less frequently subjected to stresses, and has a more stable population.

We are indebted to many individuals without whose assistance this research would not have been possible. Numerous graduate and undergraduate students participated in the cruises, both as divers and deck personnel, and assisted in the laboratory, washing samples and performing preliminary sample analyses. During the course of this study several vessels were used and we thank the captains, especially Don Peavy, and crews for trying to make our jobs easier. Our deepest gratitude is expressed to Dr. Roy Hann, Division of Environmental Engineering, Texas A&M University, who, as project director and head of the division during the time this study was in progress,

Appendix 1a. Average monthly temperature, salinity and dissolved oxygen data from the offshore site

Date	Temperature			Salinity			Dissolved Oxygen	
	Surf.	Bot.	Sed.	Surf.	Bot.	Sed.	Surf.	Bot.
1977								
2 Dec	19.5	21.0	21.5	23.8	30.1			
1978								
4 Jan	14.2	14.5	15.0	33.5	33.9			
24 Feb	10.9	11.8	12.9	—	35.7			
17 Mar	14.0	14.0	14.0	32.3	—			
15 Apr	21.2	19.9	17.9	28.6	34.4			
24 May	26.4	24.8	23.2	30.2	34.9			
20 Jun	28.6	27.7	26.0	30.0	31.9			
17 Jul	30.7	27.0	25.4	31.1	35.1			
21 Aug	30.1	28.0	26.9	34.5	35.6			
27 Sep	28.1	28.6	27.4	31.5	32.0			
30 Oct	24.8	25.3	24.3	33.7	35.0		—	5.4
30 Nov	21.4	22.9	21.6	31.1	33.5		7.0	6.7
1979								
17 Jan	14.7	14.4	14.1	34.6	35.7		—	—
28 Jan	13.0	13.0	13.1	32.5	32.7		7.0	6.7
26 Feb	13.4	13.7	13.5	28.4	33.1		7.8	6.6
25 Mar	18.2	17.2	17.1	26.4	35.2		6.0	5.6
24 Apr	23.0	21.3	19.0	20.1	32.9		7.4	5.3
24 May	24.5	23.0	22.4	25.3	33.8		5.7	3.3
25 Jun	30.3	25.0	25.0	19.4	32.8		6.2	1.9
30 Jul	28.0	26.2	26.2	28.5	32.2		5.4	1.6
21 Aug	28.7	26.9	26.8	30.6	32.0		5.3	2.9
24 Sep	24.5	25.5	25.5	24.7	28.7		6.4	4.8
18 Oct	25.1	24.7	25.0	30.3	31.6		5.6	5.5
15 Nov	19.9	20.5	20.7	30.0	30.5		6.1	6.1
16 Dec	14.2	14.5	16.0	29.0	30.2		7.0	6.8

Appendix 1a. *continued*

Date	Temperature			Salinity			Dissolved Oxygen	
	Surf.	Bot.	Sed.	Surf.	Bot.	Sed.	Surf.	Bot.
<i>1980</i>								
18 Jan	15.3	15.2	16.5	28.8	30.5		6.9	6.7
13 Feb	13.7	14.1	14.1	30.7	31.5		7.4	7.5
10 Mar	16.0	16.0	15.9	26.7	31.3		7.6	7.1
20 Mar	16.3	16.1	16.0	30.5	31.9		8.0	7.9
3 Apr	18.6	18.0	18.0	26.3	29.4	32.0	8.1	7.2
21 Apr	21.1	19.3	19.0	30.5	36.0	34.7	8.0	7.9
22 May	24.3	23.3	22.4	27.0	30.3	32.1	6.8	6.4
30 Jun	28.0	24.6	23.3	34.8	35.1	35.3	6.6	6.1
24 Jul	28.6	28.5	28.0	35.7	35.6	36.4	6.6	6.4
25 Aug	30.2	29.3	29.1	31.7	32.9	34.7	6.1	4.7
4 Sep	29.4	29.4	29.4	29.1	31.6	33.0	6.2	5.9
29 Sep	28.8	28.9	29.0	28.7	32.9	32.1	7.1	6.0
23 Oct	23.9	25.2	25.0	30.5	33.7	33.1	7.2	6.4
5 Dec	16.4	16.6	17.0	32.3	32.7	34.4	7.5	7.3
<i>1981</i>								
15 Jan	13.6	14.2	14.2	32.1	33.7	34.5	8.4	7.9
14 Feb	12.2	12.7	12.1	31.9	32.2	34.1	10.2	10.1
14 Mar	16.5	16.2	15.7	29.3	32.6	34.5	7.6	7.1
17 Apr	25.6	23.5	21.8	30.4	32.9	34.7	7.1	6.9
26 May	25.7	25.1	25.2	33.8	35.0	34.0	8.4	8.0
18 Jun	28.6	28.0	28.1	26.2	31.5	32.8	8.2	6.7
13 Jul	29.6	28.3	28.7	30.0	33.5	33.4	5.6	3.1
13 Aug	29.6	29.2	30.0	31.9	32.0	32.5	5.5	4.3
21 Sep	27.3	28.0	28.1	29.2	30.8	32.2	6.8	5.8
27 Oct	23.4	25.0	25.2	29.3	32.3	31.6	5.9	4.8
21 Nov	21.4	22.2	22.4	32.0	33.1	33.9	8.0	6.9
9 Dec	19.5	20.0	20.7	30.4	31.5	32.9	7.2	6.7
<i>1982</i>								
27 Jan	13.6	14.0	15.0	31.8	32.8	33.8	8.2	8.0
17 Feb	15.0	14.5	14.4	30.0	34.7	34.2	9.4	7.9
10 Mar	16.4	16.6	15.7	28.3	31.9	33.2	9.0	8.3
27 Apr	21.7	21.1	21.0	32.2	34.3	32.4	8.1	7.1
28 May	26.9	24.2	24.8	21.7	36.4	32.1	9.1	4.8
23 Jun	29.0	25.3	25.0	29.2	33.2	34.5	6.0	3.4
22 Jul	28.6	28.1	28.2	33.1	33.4	35.4	6.2	4.5
31 Aug	29.9	29.8	30.0	32.7	33.3	34.1	6.1	5.8
23 Sep	28.0	27.9	28.2	30.5	30.9	35.0	5.6	5.5
25 Oct	23.1	23.1	23.9	33.9	33.6	34.4	7.1	7.0
20 Nov	20.1	20.8	21.1	32.2	35.7	33.8	7.4	6.9
16 Dec	17.3	18.1	18.3	33.0	35.1	34.3	7.2	6.9
<i>1983</i>								
14 Jan	16.5	17.4	17.7	30.3	34.1	34.5	8.3	7.3
28 Feb	16.2	16.0	15.9	33.1	33.6	32.7	7.6	7.3
18 Mar	16.9	16.7	17.1	32.3	33.1	32.9	7.8	3.7
25 May	25.1	23.6	23.7	27.5	33.9	32.6	7.0	5.4
23 Jun	28.3	27.1	25.0	23.6	35.0	32.9	7.6	3.7
27 Jul	28.6	25.8	24.1	27.4	37.6	33.4	6.3	4.6
26 Aug	29.3	28.1	27.0	28.2	34.4	33.1	7.0	4.7
23 Sep	25.7	26.0	26.2	29.0	32.3	31.5	6.0	5.5
29 Nov	19.3	19.1	20.0	31.9	32.2	32.5	7.2	7.2
<i>1984</i>								
6 Jan	11.7	12.6	12.9	27.8	32.3	33.1	10.3	8.8
10 Feb	13.5	14.1	13.1	33.3	34.5	32.5	9.0	8.4
12 Apr	20.2	19.3	19.0	32.8	36.4	—	7.1	6.5
10 May	22.7	22.1	22.0	30.8	35.1	30.9	7.6	5.9
2 Jul	27.8	24.7	24.6	29.4	36.2	35.7	6.1	3.3
10 Aug	29.9	29.4	29.2	29.4	35.5	34.8	6.9	4.1
13 Sep	28.1	28.0	28.0	32.7	33.0	33.9	—	—

Appendix b. *Average monthly temperature, salinity and dissolved oxygen data from the nearshore site*

Date	Temperature			Salinity			Dissolved Oxygen	
	Surf.	Bot.	Sed.	Surf.	Bot.	Sed.	Surf.	Bot.
<i>1977</i>								
22 Sep	29.1	28.7	28.6	30.3	31.6			
14 Oct	23.5	23.4	24.0	28.5	28.6			
11 Nov	21.3	29.8	21.9	28.0	28.1			
15 Dec	16.1	16.8	16.8	22.8	25.2			
<i>1978</i>								
14 Feb	8.5	10.0	10.0	—	—			
20 Feb	10.2	10.8	11.3	27.8	33.5			
15 Mar	14.5	14.0	14.0	31.2	33.7			
14 Apr	21.4	20.1	18.9	26.5	30.0			
22 May	26.8	24.7	23.3	29.0	33.9			
16 Jun	29.7	28.2	25.9	28.0	33.0			
13 Jul	30.1	24.9	24.5	33.1	35.2			
31 Aug	29.4	30.5	29.4	28.3	29.9			
28 Sep	28.0	28.0	26.2	25.1	26.7			
25 Oct	24.6	24.2	25.0	31.4	32.5		—	6.0
1 Dec	20.3	21.3	21.1	25.7	31.2		—	6.0
<i>1979</i>								
28 Jan	12.0	12.0	11.8	32.0	32.0		8.2	7.7
13 Feb	13.9	12.7	12.9	25.7	29.4		8.8	7.2
5 Apr	20.7	21.4	18.7	23.5	26.5		6.5	5.7
26 Apr	23.1	22.0	20.7	22.7	31.1		5.5	5.0
1 Jun	25.6	24.6	24.4	24.3	27.5		5.5	2.5
28 Jun	29.3	25.0	24.3	19.9	32.0		5.6	0.7
2 Aug	28.1	27.5	26.8	28.0	30.4		4.9	3.3
23 Aug	28.0	27.8	28.2	27.6	30.8		5.4	3.2
26 Sep	24.1	25.0	25.6	22.5	28.4		6.3	4.5
29 Oct	23.0	23.1	23.9	26.7	30.3		6.3	4.8
19 Nov	19.1	19.5	20.5	27.1	29.4		6.3	5.4
19 Dec	13.6	14.2	13.7	26.7	28.4		7.6	6.9
<i>1980</i>								
28 Jan	13.3	13.8	16.3	24.1	25.1		7.5	6.7
28 Feb	14.1	13.4	14.5	29.1	30.9		7.3	6.9
31 Mar	17.8	17.6	17.8	26.2	28.2		8.4	7.9
23 Apr	20.2	19.0	19.0	31.9	34.4	34.1	7.2	6.4
28 May	26.7	24.1	23.3	24.6	31.5		7.7	4.7
2 Jul	28.5	25.8	24.0	34.8	35.0		6.4	6.6
29 Jul	28.8	28.8	28.3	35.0	35.1		6.0	6.0
27 Aug	29.3	29.0	28.4	32.5	32.5		6.6	6.6
8 Oct	25.5	25.4	26.0	29.1	29.3		6.7	6.4
4 Nov	21.2	21.2	22.1	29.3	30.8		8.2	6.8
12 Dec	14.8	15.5	14.5	29.9	31.2		8.4	7.9
<i>1981</i>								
21 Jan	10.3	11.4	13.5	31.0	32.6	32.7	9.7	9.3
18 Feb	13.4	13.3	12.9	32.4	31.7	33.8	8.4	8.0
17 Mar	17.6	17.1	16.0	29.2	34.4	—	8.2	7.4
27 Apr	23.0	22.9	23.7	29.4	30.0	32.2	5.9	5.3
27 May	25.9	25.0	25.0	29.6	31.5	30.6	8.7	7.7
22 Jun	28.9	27.5	28.0	27.3	34.0	32.7	6.8	4.2
20 Jul	29.8	27.9	30.0	30.0	33.6	31.2	6.0	3.0
20 Aug	31.0	30.3	27.6	32.0	32.0	28.4	6.0	3.3
22 Sep	27.1	27.4	24.5	27.8	28.7	28.6	5.7	5.3
28 Oct	22.8	24.5	23.1	28.4	30.3	32.0	6.7	4.8
23 Nov	21.4	22.4	19.4	32.3	33.9	31.4	7.1	5.3
10 Dec	19.0	19.1		29.8	30.2		7.5	7.2
<i>1982</i>								
24 Feb	16.9	16.2	15.0	30.0	31.2	33.0	8.3	7.5
10 Mar	17.4	16.9	15.6	28.6	31.2	32.3	8.4	8.1

Appendix b. continued

Date	Temperature			Salinity			Dissolved Oxygen	
	Surf.	Bot.	Sed.	Surf.	Bot.	Sed.	Surf.	Bot.
27 Apr	21.6	21.0	21.0	26.6	32.4	29.1	9.7	7.0
28 May	28.0	24.2	25.0	18.7	34.4	31.1	9.1	3.6
23 Jun	29.1	25.2	25.0	30.3	33.1	33.5	5.7	2.4
22 Jul	28.8	28.3	29.0	32.5	32.9	34.8	6.3	4.8
31 Aug	30.0	30.0	30.0	33.8	33.6	—	6.0	5.7
23 Sep	28.0	28.1	29.2	23.7	29.2	31.7	7.7	5.9
25 Oct	22.8	22.5	24.0	33.8	34.0	31.9	7.2	7.2
20 Nov	20.7	20.4	21.0	31.9	35.7	32.2	7.5	6.9
1983								
18 Feb	15.4	15.1	15.0	22.8	30.1	28.3	8.9	8.0
18 Mar	16.5	16.3	16.2	30.4	31.8	31.8	7.9	7.3
25 May	24.9	23.9	23.5	21.4	32.0	—	8.2	5.0
23 Jun	28.7	27.6	25.0	18.4	32.8	30.0	7.6	1.5
27 Jul	29.0	26.1	25.4	26.6	32.5	32.6	6.2	3.7
26 Aug	29.5	28.1	28.0	27.0	30.2	—	6.7	5.0
27 Sep	25.1	25.5	26.0	25.6	30.2	28.0	6.3	5.5
1984								
6 Jan	11.9	12.9	12.0	27.0	30.0	32.0	11.2	9.1
10 Feb	13.3	12.3	13.3	28.6	31.5	31.3	7.6	7.0
12 Apr	20.8	19.1	19.0	33.0	35.7	—	7.0	5.6
10 May	23.2	22.6	22.6	27.9	30.7	28.0	8.2	5.1
2 Jul	27.7	24.7	25.0	31.4	35.6	35.0	6.0	2.5
10 Aug	31.2	30.0	29.3	30.1	34.1	32.5	6.1	5.1

* averages from this date forward are from 5 stations.

made funds available to continue sampling on a regular basis after project funding was reduced to allow only quarterly sampling. Robert Case, James Cummings and Gary Wolff, data managers on the study, assisted in analysis of data by computer.

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